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Homogeneity of coral reef communities across 8 degrees of latitude in the Saudi Arabian Red Sea

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ABSTRACT:

Coral reef communities between 26.8°N and 18.6°N latitude in the Saudi Arabian Red Sea were surveyed to provide baseline data and an assessment of fine-scale biogeography of communities in this region. Forty reefs along 1100 km of coastline were surveyed using depth-stratified visual transects of fish and benthic communities. Fish abundance and benthic cover data were analyzed using multivariate approaches to investigate whether coral reef communities differed with latitude. A total of 215 fish species and 90 benthic categories were recorded on the surveys. There were no significant differences among locations in fish abundance, species richness, or among several diversity indices. Despite known environmental gradients within the Red Sea, the communities remained surprisingly similar. The communities do, however, exhibit subtle changes across this span of reefs that likely reflect the constrained distributions of several species of reef fish and benthic fauna.

KEYWORDS: Benthic cover, Biogeography, Coral reef fishes, Dissimilarity, Red Sea

INTRODUCTION:

The Red Sea is located in the northwest periphery of the Indian Ocean and has long been recognized as its own biogeographic region and a hotspot for biodiversity (Goren & Dor, 1994; Randall, 1994; Randall, 1998) with high levels of endemism (Briggs, 1974; Spalding *et al.*, 2007; Briggs, 2012; Bowen, 2013; Kulbicki *et al.*, 2013, DiBattista *et al., in press*). Some of the earliest tropical marine expeditions were conducted in the Red Sea, where pioneering naturalists described marine fauna which was also representative of the greater Indian Ocean (Forsskål 1775; Rüppell, 1828; Cuvier, 1828; Ehrenberg, 1834; Klunzinger, 1870). More recently, with the exception of the Gulf of Aqaba, there has been relatively little ecological research in the Red Sea compared to other major tropical reef systems (Berumen *et al.*, 2013). The lack of baseline information on fish populations and species ranges within much of the Red Sea hinders attempts to quantify changes in the local ecology due to environmental fluctuations or increasing anthropogenic influences.

In addition to its unique set of fauna, the Red Sea is also recognized as a mostly thriving coral reef ecosystem coexisting within relatively extreme environmental conditions (Sheppard *et al.*, 1992). Only the Arabian Gulf supports coral reef environments that experience higher temperatures and salinity levels than those located in the Red Sea (Sheppard *et al.*, 1992). However, across this long and narrow body of water, which spans 17 degrees of latitude, the Red Sea is not homogenous. Sea surface temperatures (SST), salinity, and nutrient concentrations exhibit latitudinal gradients and fluctuate seasonally (Acker *et al.*, 2008; Ngugi *et al.*, 2012; Raitsos *et al.*, 2013). Average temperatures increase southward and range from 20-28 °C (north to south) in the winter

and 26-32 °C (north to south) in summer. The low rainfall and freshwater influx in this hot, arid region and pronounced evaporation rates result in high salinity levels (~41psu) which decrease (to 36psu) near the Bab al Mandeb Strait, the only connection to the Indian Ocean (Murray & Johns, 1997). Nutrient levels in the Red Sea also increase from north (chlorophyll-a= 0.03 [mg m^{-3}]) to south (10 [mg m^{-3}]), with the most oligotrophic northern waters characterized by high visibility in contrast to the more turbid southern region (Sheppard & Sheppard, 1991).

The Red Sea has recently been described as containing two marine ecoregions (Spalding *et al.*, 2007), with a division in the central Red Sea located near 20°N latitude. This simplified delineation is contentious among some researchers familiar with the region. Nonetheless, it provides a framework for us to test a hypothesis. While levels of endemism are key characteristics for establishing broader biogeographical provinces and realms (Briggs, 1974a; Briggs, 2012; Spalding *et al.*, 2007), the finer-scale marine ecoregions such as those identified within the Red Sea are defined as "areas of relatively homogeneous species composition, clearly distinct from adjacent systems…[and] determined by a distinct suite of oceanographic or topographic features" (Spalding *et al.*, 2007). However, the available data from this region is focused only on a few taxonomic groups. For example, regional chaetodontid and pomacanthid distributions were explored by Roberts *et al.* (1992) and Righton *et al.* (1996) while Sheppard & Sheppard (1991) and DeVantier & Pilcher (2000) have published studies on the distribution of scleractinian assemblages within the Red Sea. While these previous studies provide valuable insight to species- and family-level distributions and patterns, they may not be sufficient to characterize ecoregion boundaries. Large-scale biogeographic trends provide

insights into broad ecological processes and relationships to changing environmental conditions; understanding these trends facilitates the establishment of sound management plans. The present study provides an overview of biogeographic patterns of reef communities for this region.

The aims of this study were: 1) to determine if and to what degree offshore reef communities change along a latitudinal gradient within our study area, 2) to explore the presence of a within-Red Sea ecological boundary at 20°N as described by Spalding et al. (2007), and 3) to provide baseline data on the biogeography of coral reef communities for future comparative studies in the Red Sea. To achieve these goals, surveys were conducted on coral reefs in the Saudi Arabian Red Sea spanning 1100km of latitudinal coastline. Surveys assessed the abundance of reef fish species as well as benthic cover at 40 coral reefs. In addition to providing a valuable dataset of distributions and abundances, this data lays the foundation for investigations of the mechanisms underlying regional biogeography.

METHODS

Ecological survey data collection:

Our study area consisted of 40 offshore reefs along the Saudi Arabian coastline between 26.8°N and 18.6°N latitude (Figure 1). Survey sites were selected to reduce the confounding effects of reef type, reef slope, and within-reef location of transects. Reefs were chosen based on their position at the edge of the Arabian shelf and near deep drop-offs, with survey sites located near the outer reef slope on the leeward side of the reef (given predominant northwesterly winds in the Red Sea, this meant that our surveys were

conducted on the southern ends of the reefs). Reef sites varied between 7 and 81km from shore, representing the variable width of the continental shelf in the Red Sea (Figure 1). The lack of any significant rainfall (yearly average less than 70mm (DeVantier & Pilcher, 2000)), the near absence of freshwater runoff, and minimal coastal development (especially in the north) greatly reduces the confounding effects of varying reef distance from shore. We define the terminology used in this study as follows. “Sub-region” refers to the subdivisions of the Red Sea that we surveyed (i.e., the northern, central, or southern sites within the Red Sea), “section” to refer to the groupings of reefs, and finally, we refer to each individual reef site as “reef”. We surveyed four reefs per section with a total of 10 sections that were further grouped into three sub-regions (Table 1). These sub-regions were defined as: “northern” (n=12 reefs; 26.8°N – 24.4°N), “central” (n=16 reefs; 23.8°N – 21.8°N), and “southern” (n=12 reefs; 19.8°N – 18.6°N) (see Figure 1 and Table 1). The groupings by sub-region were used to identify differences within our study area for a biogeographic context, while the sections were used to investigate finer-scale spatial variation in community indices.

At each reef, four replicate transects were laid at each of four depths: the reef crest (~0m), 2m, 6m, and 10m, for a total of 16 transects per reef (as per Jones *et al.*, 2004). All species (Appendix S1) were counted on 50m x 4m belt transects with the exception of the damselfishes (family Pomacentridae) which were surveyed within a 2m belt transect, as well as the gobies (family Gobidae), blennies (family Blennidae), and dottybacks (family Pseudochromidae), which were surveyed within a 1m belt due to their small size and abundance. For each transect, three divers (MIM, PLM, and either GPJ or MLB) observed and recorded the abundance of specific groups of fishes based on their

expertise. Prior to other analyses, count densities were standardized to 200m^2 (hereafter referred to as 'abundance'). A fourth diver (SN) conducted point-intercept benthic surveys along the same 50m transects, recording the benthos at 100 random points selected by a random number generator that allowed for at least two points to be within the bounds of each meter of the transect to space the points out across the entire transect. The substratum under each point was identified to the lowest taxonomic group and morphotype where possible (Appendix S2).

Statistical Analyses

Community indices

Several community indices were assessed among the three latitudinal sub-regions in our study. As each reef had the same number of transects, total abundance of all fishes surveyed within a reef were used to calculate the average total abundance of fishes in each of the three sub-regions (n = 12 or 16 reefs per sub-region). Total richness (*S*) was calculated at the reef level by tallying the number of fish species recorded on all of the 16 transects (i.e., if a fish was seen on any transect it was counted for the reef). The Shannon-Weiner diversity index (*H'*, log(e) scale) (Shannon & Weaver, 1963), Pielou's evenness (*J'*) (Pielou, 1975), and Simpson's diversity (1-λ) (Simpson, 1949) were all calculated at the reef level using PRIMER-v6 (Clarke, 2006). Values of *J'* lie between 0-1 where 0 indicates an uneven distribution of abundances among species within a site and values closer to 1 show more evenly composed communities. Similarly, Simpson's index is also on a 0-1 scale, where values near 0 are interpreted as less diverse and values approaching 1 signify high diversity. All of the aforementioned indices were compared

for significant differences among the three sub-regions using one-way way Analysis of Variance (ANOVA) in R v3.03 (R Core Team, 2014).

Multivariate analyses among reefs

We also analyzed assemblage and biogeographic patterns in the data using non-metric multi-dimensional scaling (NMDS; Kruskal & Wish, 1978) to display the relative dissimilarity distances based on community compositions among the 40 reefs. For this and all subsequent multivariate analyses, data were analyzed at the reef level (treating the 16 transects as replicates within a reef). Fish abundance data and percent benthic cover data were square root transformed to balance the effect of disproportionately abundant species prior to conducting the analyses. The NMDS plots were calculated using the resemblance matrix of Bray-Curtis similarity coefficients (Bray & Curtis 1957; Clark and Warwick, 2001). While there are many options for similarity indices, the Bray-Curtis method has been shown to be sensitive to differences in community structure when using species abundance data, and is thus commonly used in coral reef community studies (Burt *et al.* 2011; Dornelas *et al.*, 2006; Holbrook *et al.*, 2015). Similarity coefficients are calculated between assemblages of every pair of reefs using the average abundances of each species within the reef. Here, the Bray-Curtis similarity coefficient *S*, represents the similarity between reefs *j* and *k* where y_{ij} represents the average abundance of the species in column *i* and reef *j*.

$$S_{jk} = 100\left\{1 - \frac{\sum_{i=1}^{p}|y_{ij} - y_{ik}|}{\sum_{i=1}^{p}(y_{ij} + y_{ik})}\right\}$$

Multivariate analyses among sub-regions

To determine if any biogeographic differences were evident, reef sites were analyzed based on the groupings by the previously defined northern, central, and southern sub-regions and assessed to determine if communities were similar among sub-regions. Analysis of similarity (ANOSIM; Clarke, 2001) was conducted on both the fish and benthic resemblance matrices to test the null hypothesis that the community assemblages were similar throughout the three sub-regions. In the ANOSIM significance test, the resulting global *R*-value lies between –1 and 1 and reflects the degree of similarity between the pairwise tests between the three sub-regions. The more similar reef communities within sub-regions are to each other than to those in other sub-regions, the closer the value of *R* approaches 1. Positive values nearer to zero indicate that some reefs between sub-regions show more similarity than reefs within the same sub-region, while a negative *R* value would indicate that reefs between sub-regions are more similar to each other than within the three sub-regions (Clarke, 2001).

A pairwise comparison of similarity percentages (SIMPER; Clarke, 2001) of abundance data between sub-regions was used to determine which species and benthic components contributed most to the differences between sub-regions. This analysis first identifies the species that are most influential in characterizing a sub-region, and then ranks the species that drive average dissimilarity between them. Species with greater relative abundances are more heavily weighted in SIMPER calculations.

Correlations between fish and benthos

To test whether relationships between abundances of fish taxa versus benthic components exist, we used the RELATE (Clarke, 2001) analysis with Spearman's rank

method. This analysis shows how well the fish resemblance matrix correlates with the benthic matrix. Spearman's rank correlation (ρ) is a measure of the degree of correlation between the two resemblance matrices, calculated by matching every variable in one matrix to every variable in the other matrix then creating a ranking based on the similarity of ρ values between benthic categories and fish species across sites. Once patterns were detected, BEST (BVSTEP) analysis (Clarke, 2001) used this ranking to identify which of the benthic variables most strongly correlated with fish community compositions. Due to the large number of variables, we used benthic categories that contributed at least 1% of dissimilarity between regions as identified by the SIMPER analysis (41 of 90 categories). These analyses are commonly used to distinguish between different communities and to identify geographic sub-regional breaks (Khalaf & Kochzius 2002, Burt *et al.*, 2011; Sales *et al.*, 2012). All multivariate and correlation analyses were conducted using PRIMER 6+ PERMANOVA software (PRIMER-E v6; Clarke, 2006).

RESULTS

Community indices

A total of 268,313 individuals were counted representing 215 species from the 40 reefs (Appendix S1). However, nine fish taxa were subsequently removed from further analysis because they were not identified to species and an additional four species, all within the family Mullidae, were also excluded, as they were not counted in all of the survey periods (Appendix S3). The remaining 202 fish species, representing 110 genera and 26 families were used for subsequent analyses (Appendix S1 and S2).

Total abundance was not significantly different across sub-regions (one-way ANOVA, $F_{2,37}$=2.76, p=0.0764). Similarly, the other community indices showed no significant differences among sub-regions. These included mean species richness (one-way ANOVA, $F_{3,37}$ = 1.319, *p*=0.280) (Figure 2b), Shannon's diversity (*H'*) (one-way ANOVA, $F_{2,37}$ = 0.585, *p* = 0.562), Pielou's evenness (*J'*) (one-way ANOVA, $F_{2,37}$ = 0.437, *p*=0.649), and Simpson's index (*1-λ')*(one-way ANOVA, $F_{2,37}$ = 1.487, *p* =0.239 (Figure2b-d).

Among the individual reefs, the highest and lowest values of Shannon's diversity, Pielou's evenness, and Simpson's index were within the central sub-region. *Abu Terr* reef in the region of North Jeddah had the highest indices with *H'*=3.15, *J'*=0.69, and *1-λ'*=0.91, while the lowest values were found on *Shib Shabarir* in the Seven Sisters area with *H'*=1.37, *J'*=0.31, and *1-λ'*=0.56 (Table 2).

Fish assemblage multivariate analyses across reefs and between sub-regions

The NMDS plot (Figure 3) for fishes within reefs revealed the clustering of northern and southern sites separated by a wide band of central reef sites, generally showing a gradual progression of community assemblages from north to south. Pairwise ANOSIM tests by sub-region also confirmed significant differences between the three sub-regions (p<0.001, R=0.321) (Table 2). The benthic NMDS plot (Figure 3) also shows clustering of reef sites based on sub-regions. Benthic ANOSIM results confirmed that sub-regional clusters are significant (p<0.001, R=0.632) with all pairwise tests yielding *P* values of 0.001 (Table 3).

However, in the SIMPER pairwise comparisons, four species (*Pseudanthias squamipinnis, Chromis dimidiata, Chromis flavaxilla*, and *Pseudochromis fridmani*) were

consistently identified as being the primary drivers of between-sub-region dissimilarity (Table 2). The three sub-regions were also characterized by a similar assemblage of fishes with the same 19 species making up the top 25 most influential species driving the similarities within each of the three sub-regions (Table 4). None of the three sub-regions were found to have a notably distinct assemblage structure based on pairwise dissimilarity values. SIMPER results show that benthic categories driving the top 25% of differences in the ANOSIM were more diverse than the combinations that drive differences in the fish ANOSIM (Tables 2 and 3). Percent contribution levels were also more even and were generally higher among these benthic factors than contributions found in the fish community (Tables 2 and 3). As in the fish assemblages, low dissimilarity values indicate relatively low levels of differences among sub-regions.

Correlations between fish and benthos

The RELATE analysis showed a significant positive correlation between patterns in the fish assemblages and the corresponding benthic communities ($p<0.001$, $\rho=0.386$). The SIMPER analysis identified that 41 of the 90 benthic categories contributed at least 1% to dissimilarity in benthic communities. We therefore used BEST (BVSTEP) to examine these 41 benthic variables in order to identify which benthic variables may have contributed to shifts in the fish assemblages. However, this analysis did not find a benthic variable or a combination of benthic variables that correlated significantly ($p=0.07$) with the changes in fish assemblages across latitude.

DISCUSSION

263 Previous large-scale studies of biogeographic patterns were conducted primarily
264 on near shore reefs in the Red Sea and had revealed a trend of higher diversity in what
265 corresponds to the northern and central sub-regions in our study (Roberts *et al.*, 1992;
266 Sheppard & Sheppard, 1991). These studies also identified overall latitudinal changes in
267 the species composition of selected taxa such as the chaetodontids, pomacanthids and
268 sclerictinians (Roberts *et al.*, 1992; Sheppard & Sheppard, 1991). Our extensive surveys
269 of 40 reefs along 1100km of the Saudi Arabia Red Sea coast encompassing 110 genera of
270 fishes and 90 benthic categories, presents a novel dataset representing offshore reef
271 communities. Though we do not directly compare our data to the findings in previous
272 literature on inshore reefs, our study revealed that across latitude, offshore reef fish
273 assemblages were generally more homogenous in nature. While there were subtle
274 assemblage shifts along this gradient, they were not strong enough to be reflected in five
275 common indices, none of which differed significantly among the three sub-regions.
276 Nevertheless, reefs within the same area generally cluster closely together in an overall
277 latitudinal pattern. Patterns found in the fish assemblages also appear to be related to
278 benthic composition, but the exact drivers are difficult to identify. We did not find strong
279 evidence for the current location of the within-Red Sea ecoregion boundary designated by
280 Spalding *et al.* (2007) at 20°N.
281 The great deal of homogeneity and relatively small differences in the species that
282 characterize the reefs throughout our study area are in contrast to earlier studies on near-
283 shore reefs and contradict the delineations of distinct bioregions assigned in the MEOWS
284 (Roberts *et al.*, 1992; Spalding *et al.*, 2007). Subtle shifts are, however, apparent in the
285 fish assemblage ordination clustering the reefs in a generally latitudinal order. Northern

reefs, as well as some southern reefs, were highly clustered within their respective sub-regions while many central and some southern reefs were grouped together also indicating a gradual latitudinal shift. These patterns can be attributed to the several species that have restricted ranges within the Red Sea, an effect already reported within the chaetodontid family (Roberts *et al.*, 1992). Several butterflyfishes exhibit distributions that are confined to either the northern, southern, or central sub-regions (e.g., Roberts et al. 1992). Although there were no apparent major habitat changes that would limit these distributions, a more thorough examination of specific case studies and habitat associations might reveal further connections

There is no standard value for a threshold of difference vs. similarity, however, it is our opinion that the results indicate relatively homogenous communities (cf. Burt *et al.*, 2011). We did not find evidence supporting the current division of the Red Sea into two bioregions at 20 °N latitude, based on the definition used by Spalding *et al.* (2007). The lack of separate clusters between sites across this delineation (between central and southern sub-regions) and the uniformity in species driving the similarities within sub-regions indicated a generally homogeneous assemblage along this span of coastline. We also found that dissimilarities (though significant) were half that of similar studies comparing coral reef fish assemblages across other similarly defined bioregions that displayed substantially higher dissimilarity percentages (e.g., 72-85%) (Burt *et al.*, 2011). This was further corroborated by the high resemblance of the fishes (19 of the 25 species identified by SIMPER analyses) that contribute to the similarity between each sub-region. Across this stretch of the Red Sea, while the dissimilarities may be significant, communities remained relatively similar. Results from the ANOSIM analysis indicated

309 that fish assemblages were more similar between adjacent sub-regions than other
310 pairwise comparisons. The benthic communities formed clear clusters but with less
311 evidence of a latitudinal pattern. However, subsequent BEST analyses and careful
312 examination of the reef ordination show patterns with similar clustering between the two
313 data sets.

314 Given the lack of previously available detailed biogeographic information for
315 much of the Red Sea, and particularly offshore reefs, the placement of an ecoregion
316 boundary at 20 °N appears to be a slightly misleading conclusion arising from over-
317 simplification of previous studies (although we acknowledge that compromises by
318 Spalding *et al.* (2007) were likely necessary to keep the total number of global ecoregions
319 reasonable). Other recent investigations in the southern Red Sea provide evidence that a
320 more appropriate division may exist around 17.5 °N latitude and southwards to the strait
321 of Bab Al Mandab, where turbidity and productivity levels are much higher than the rest
322 of the Red Sea (Raitsos *et al.*, 2013). This shift in the southern Saudi Arabian Red Sea
323 coincides with a distinct habitat change. An extensive network of coral reefs known as
324 the Farasan Banks occupies the region from ~20°N to ~18°N , while to the south from
325 ~17.5°N onwards, lies the Farasan Islands. The reef communities of the Farasan Islands
326 extend into Yemeni waters and have been described as unique among Red Sea habitats
327 (Sheppard *et al*, 1992; Turak, 2007) in that they are characterized by increasingly reduced
328 coral reef development compared to more northern Red Sea coral communities. This area
329 has shallow geomorphology that results in high SST, turbidity, and restricted water flow
330 (Turak, 2007). Although our study did not include sites in the Farasan Islands, other work
331 from this region suggests a major transition in fauna and assemblage composition. For

example, two recent studies have identified barriers to gene flow that match this shift in environmental conditions (two-band anemonefish, Nanninga *et al.*, 2014; Carter's reef sponge, Giles *et al.*, 2015). It may be more appropriate, therefore, for a within-Red Sea demarcation of bioregions to be placed between the southern end of the Farasan Banks and the beginning of the Farasan Islands. In addition, surveys along the Yemeni coast by Turak *et al.* (2007) found that the coral assemblages of the northern reefs of Yemen are more similar to the Farasan Islands while the coral assemblage in the southern area is likened to the Gulf of Aden, indicating that perhaps the Gulf of Aden bioregion should extend into the southern tip of the Red Sea.

We found that benthic communities reflected similar patterns to the fish assemblages, though the ecological relationships between such large numbers of variables in the analysis may mask any clear associations. The ordination in the two communities as well as the RELATE analysis confirm that trends exhibited by the fish assemblages were likely related to patterns found in the benthic communities. Interestingly, ordination and SIMPER results showed that the northern reefs for both the fish and benthos show greater uniformity, indicating consistency of communities among those reefs. The northern sub-region is arguably the most environmentally challenging region in the Red Sea as a result of having the overall lowest productivity (Raitsos *et al.*, 2013) and highest salinity (Ngugi *et al.*, 2012). It is possible that specific niche specialization become necessary as environments become relatively more extreme (e.g., Moldenke, 1975). The result of more challenging environmental conditions may, therefore, be increased homogeneity among the resident communities. Additionally, it is also interesting that the sub-regional differences found on inshore reefs in Roberts *et al.*

(1992) appear to be more obvious and further north than our findings at offshore reef habitats. This may suggest that the forces or gradients that determine species distribution in the Red Sea communities are more influential or stronger in near-shore communities.

Future studies could use the data presented here as a basis for more in-depth work with the aim of identifying specific mechanisms underlying the latitudinal gradient in community assemblages. For example, subsequent studies may further examine reef sites with greater habitat variability than the present study (e.g., comparing coastal fringing reefs to offshore reefs, or sheltered vs. exposed sides of a given reef). It is likely that some species exhibiting restricted ranges within the Red Sea, such as the butterflyfishes and angelfishes (Roberts *et al.*, 1992), drive the observed shifts in the assemblages along the latitudinal gradient we explored. There are further reef-scale biological mechanisms interacting with biogeographic mechanisms to produce community variation. For example, local population explosions of *Acanthaster planci*, *Drupella*, *Echinometra*, or coral disease have been known to significantly alter Red Sea reef fish and coral communities and habitat structure, (e.g., Antonius & Riegl, 1998; Khalil *et al.*, 2013; Riegl *et al.* 2012, 2013) which likely affect the fish assemblage structure. These types of disturbances have previously been suggested as a potential homogenizing force in Red Sea reefs (Riegl *et al*. 2012). Future work and repeated observations will be required to confirm this hypothesis.

CONCLUSION

Red Sea reef fish assemblages along the northern two-thirds of the eastern Red Sea are, for the most part, composed of similar assemblages of species with no dramatic

changes in the general communities along this latitudinal gradient when comparing reef communities on the edge of the continental shelf. Nevertheless, shifts do occur, likely driven by the respective range limits of several species that are confined to either the northern or southern Red Sea. While we recognize that ecoregion delineation is not a fully quantitative endeavor, we recommend that the previously described zonation in Spalding et al.'s Marine Ecoregions of the World within the Red Sea be reconsidered. This central bioregion lacks clearly distinct species compositions on either side of its borders, and as such may not be a reasonable biogeographic demarcation. Due to well-established differences in abiotic conditions as well as habitat structure and geomorphology, we suggest that more studies be conducted comparing the fauna between the far southern region (below 18° latitude and continuing to the strait of Bab Al Mandab) and the rest of the Red Sea including, the western side. While we were not able to explore this possibility at the present time, our study provides a useful dataset from well-distributed sites along the eastern Red Sea. Given global challenges associated with "shifting baselines" (Pauly, 1995) and the emerging evidence of overfishing effects in the Saudi Arabian Red Sea (e.g., Jin *et al.*, 2012; Spaet & Berumen, 2015), some form of recent reference data from this region is needed. This dataset could form the basis for later work to investigate finer-scale relationships between fish, benthos, and abiotic factors to understand the ecological mechanisms driving biogeographic patterns within the Red Sea.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1: Summarized densities of reef fish by section, surveyed in visual belt transects in the Saudi Arabian Red Sea. Values are standardized as estimated abundance (± SE) per 200m^2. The 202 species presented here were used in analysis of biogeographic patterns within the Saudi Arabian Red Sea. Each section is composed of 4 reefs and each reef contained 16 replicate transects (i.e., presented here are the means of 64 transects for each section).

Appendix S2: Summarized results of benthic cover by section, surveyed in point-intercept transects in the Saudi Arabian Red Sea. Values are standardized as estimated percent cover (± SE). Categories reflect the highest level of taxonomic identification used in the surveys. The 90 categories presented here were used in analysis of biogeographic patterns within the Saudi Arabian Red Sea. Each section is composed of 4 reefs and each reef contained 16 replicate transects (i.e., presented here are the means of 64 transects for each section).

Appendix S3: Species or taxonomic categories recorded in reef fish surveys in the Saudi Arabian Red Sea that were excluded from analyses. The justification for excluding each category is indicated.

BIOSKETCH

The RES team (SRT, GPJ, MIM, PLM, SN, MLB) conducted these surveys as part of a WHOI-KAUST partnership, with this project specifically aiming to create some form of baseline data for future work at KAUST. The Reef Ecology Lab at KAUST (MBR, VSNR, MLB) is interested in generally understanding Red Sea ecology, particularly in a comparative context to other Indo-Pacific reef systems.

Author contributions: SRT, GPJ, MIM, PLM, SN, MLB collected the data. MBR analyzed the data. SRT and MLB provided funding. MBR and MLB wrote the manuscript. All authors contributed to manuscript sections or general editing.

570 **FIGURE LEGENDS**

571 **Figure 1.** Reef sites surveyed in the Red Sea for fish abundance and benthic cover, with
572 northern (green triangles), central (dark blue circles), and southern (cyan squares),
573 groupings of survey sites. Reefs were numbered (shown next to reefs) in order of latitude
574 and these correspond to the numbers in Table 1.

575 **Figure 2.** Community indices for fish assemblages at 40 reefs in the Saudi Arabian Red
576 Sea as recorded using ecological survey data. The 40 reefs were grouped by the three
577 sub-regions defined as: "northern" 26.8° – 24.4° N (n = 12 reefs), "central" 23.8° – 21.8°
578 N (n = 16 reefs), and "southern" 19.8° – 18.6° N (n = 12). Each reef contained 16
579 transects A) Mean abundance of all recorded individuals per reef (all transects totaled at
580 each reef). B) Mean total species richness (*S*) recorded on each reef. C) Mean Shannon-
581 Weiner diversity index (*H'*) (log(e) basis) values. D) Mean Pielou's evenness (*J'*) values.
582 All boxplots show the mean (bold line) with the upper and lower quartiles while whiskers
583 indicate the maximum and minimum values found on the reefs within each section of the
584 coastline.

585 **Figure 3**. Cluster analysis and non-metric multidimensional scaling (NMDS) of
586 reef communities at 40 reefs in the Saudi Arabian Red Sea. Each reef contained 16
587 transects on which abundance of 202 species of fishes were recorded and benthic
588 cover determined. Fish abundance data were square-root transformed prior to
589 creating the resemblance matrix. A) Cluster analysis of the 40 reefs based on fish
590 abundances. B) Cluster analysis of the 40 reefs based on percent cover of benthic
591 categories. C) NMDS of fish assemblages. The two-dimensional distance between
592 sites signifies the relative degree of difference between assemblages. D) NMDS of

benthic communities. Colors and shapes denote geographical assignments to one of three sub-regions: Northern sites (1-12, green triangles), central sites (13-29, dark blue circles), and southern sites (30-40, light blue squares).

TABLE CAPTIONS

Table 1. Details of 40 Saudi Arabian Red Sea coral reefs surveyed. Surveys were conducted in three general sub-regions of the Red Sea. Ten regions were surveyed, each comprised of four reefs. Reefs were assigned a numerical code (1-40) in order of latitude and used in subsequent figures. Longitude and latitude indicate survey location on reef. Distance from shore is also reported and shows the straight-line distance to the nearest point on land. The total number of fish species (S) recorded on 16 belt transects (4 each at the crest, 2m depth, 6m depth, and 10m depth) using visual surveys are reported, along with other community indices: *J'*, indicating Pielou's evenness; *H'*, representing Shannon's Diversity index; and *1-λ*, representing Simpson's Diversity index.

Table 2. Similarity results of reef fish assemblages determined using SIMPER and ANOSIM analyses. The tables show the species cumulatively contributing to the top 25% of the dissimilarity in each pairwise comparison (SIMPER) of three sub-regions from the Saudi Arabian Red Sea. Relative contribution and the cumulative contribution of the top species to sub-regional dissimilarity as well as the mean abundances for each species in each sub-region are shown for comparison. All other species each contributed <2% of differences in assemblages. Percent dissimilarity in addition to overall ANOSIM comparison results (Global R= 0.321, $p<0.001$) are included alongside the pairwise results, also presented here.

Table 3. Similarity results of benthic communities determined using SIMPER and ANOSIM analyses. The tables show the benthic categories cumulatively contributing to the top 25% of the dissimilarity in each pairwise comparison

621 (SIMPER) of three sub-regions from the Saudi Arabian Red Sea. Relative
622 contribution and the cumulative contribution of the top benthic group to sub-
623 regional dissimilarity as well as the mean percent cover for each in the three sub-
624 regions are shown for comparison. All others contributed <2% of differences in
625 communities. Percent dissimilarity in addition to overall ANOSIM comparison
626 results (Global R= 0.632, $p<0.001$) are included alongside the pairwise results, also
627 presented here.

628
629 **Table 4.** The most influential coral reef fishes out of the 200 species included in the
630 analysis driving *similarities* (using SIMPER analysis) between three regional sub-regions
631 which are defined as: “northern” 26.8°N – 24.4°N (n=12 reefs), “central” 23.8°N –
632 21.8°N (n=16 reefs), and “southern” 19.8°N – 18.6°N (n=12 reefs). This list is a
633 compilation of the top 25 species characteristic of each individual sub-region based on
634 the total abundance in the sub-region. Marked cells denote whether that species was
635 identified as a primary driver of similarity within that sub-region.
636
637

TABLES & FIGURES

Figure 1.

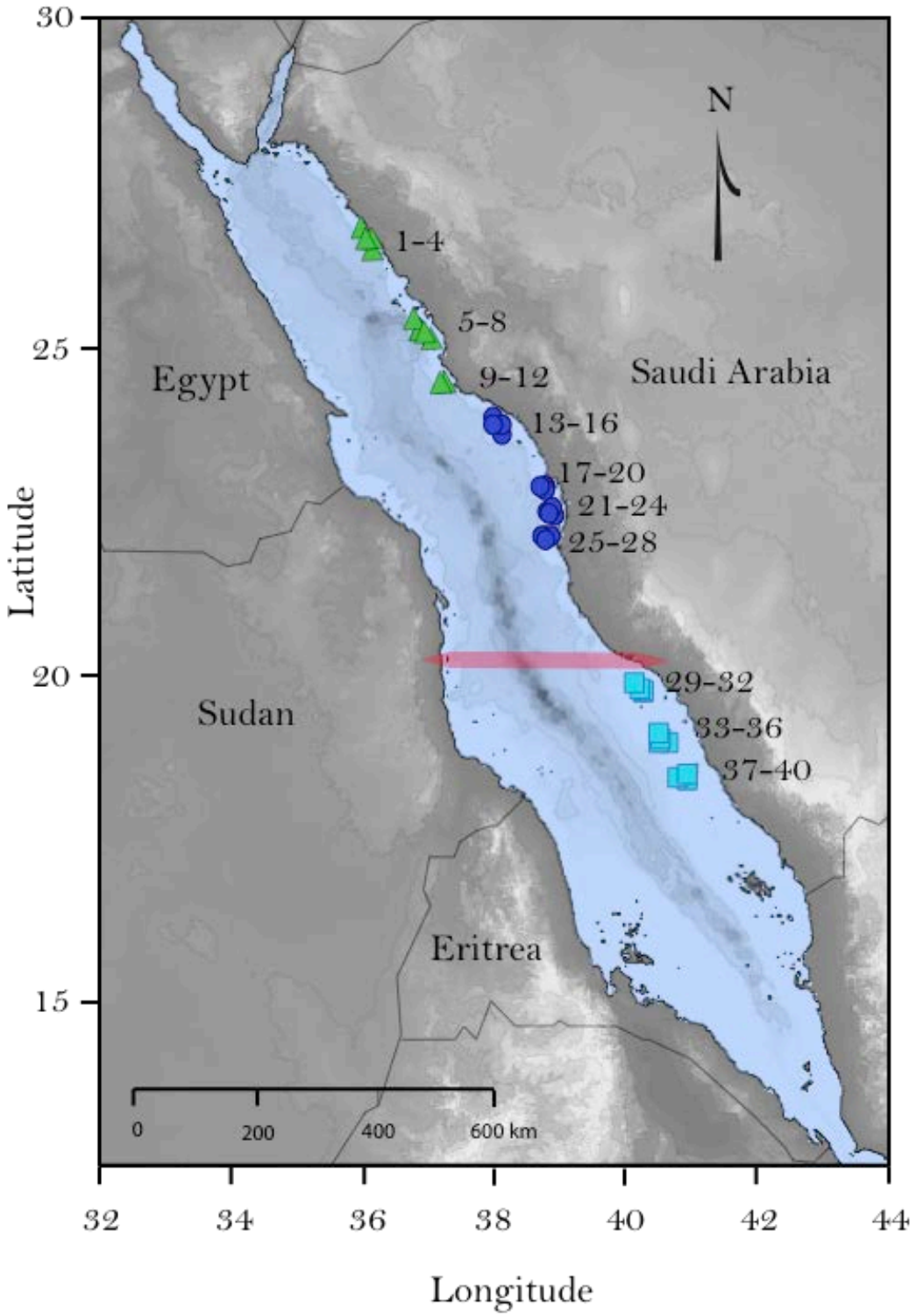

Figure 2

Figure 3.

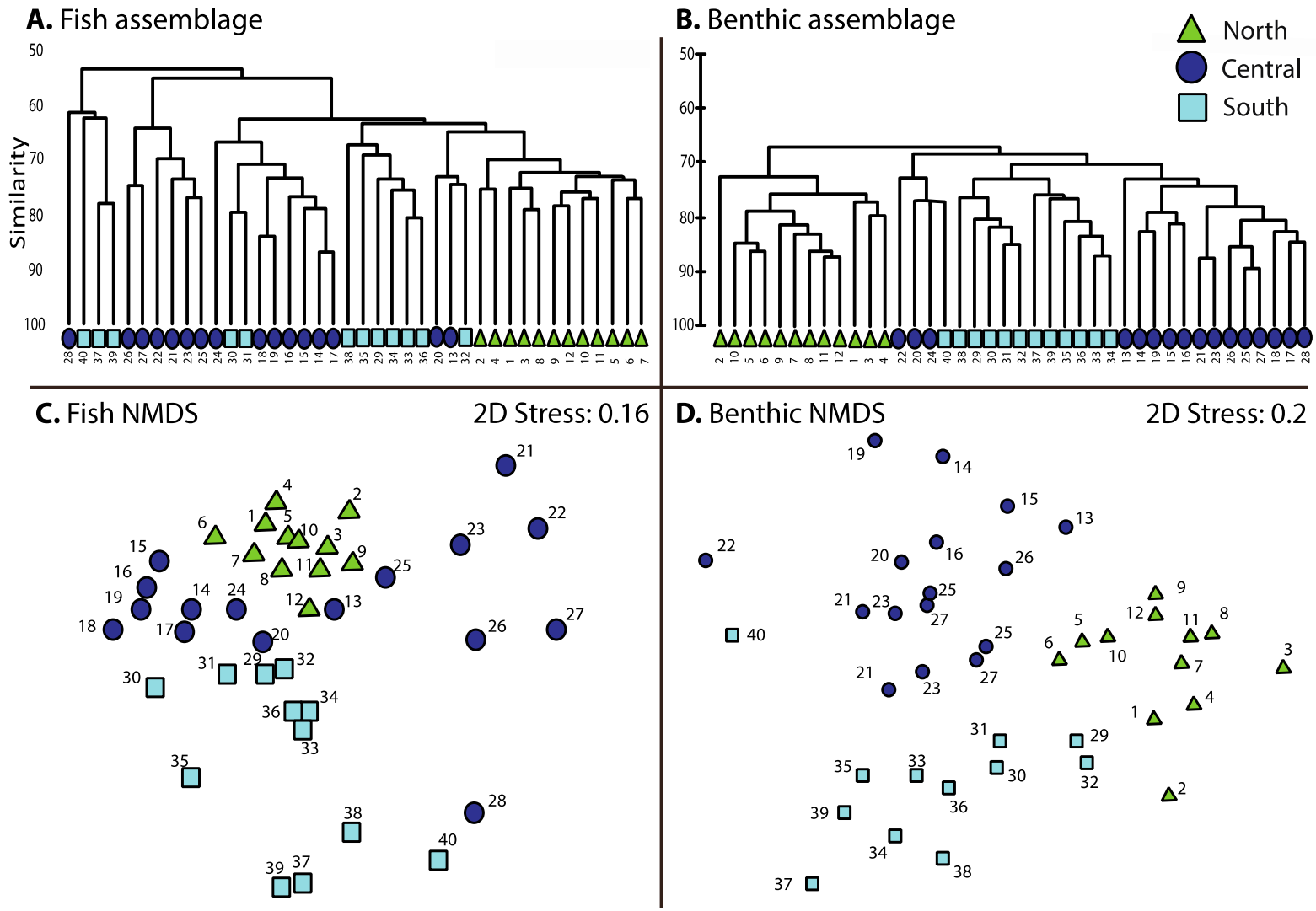
A. Fish assemblage
B. Benthic assemblage
Similarity
50
60
70
80
90
100
North
Central
South
C. Fish NMDS
2D Stress: 0.16
D. Benthic NMDS
2D Stress: 0.2

Table 1.

Sub-region	Reef ID #	Section	Reef Name	Latitude	Longitude	Survey Year	Dist.(km)	S	J'	H'(loge)	1-Lambda'
North	1	Wajh	Pele 1	26.80908	35.89095	2011	16.0	68	0.41	1.72	0.62
	2	Wajh	Skharu Luhs 1	26.62883	36.25481	2011	8.10	93	0.51	2.30	0.72
	3	Wajh	Skharu Luhs 3	26.40832	36.26557	2011	9.6	87	0.47	2.09	0.71
	4	Wajh	Skharu Luhs 2	26.37708	36.25453	2011	9.6	86	0.50	2.23	0.78
	5	Wajh Bank	Wajh Bank 1	25.39082	36.68348	2011	34.3	85	0.58	2.58	0.80
	6	Wajh Bank	Wajh Bank 2	25.27030	36.85697	2011	25.2	78	0.47	2.07	0.74
	7	Wajh Bank	Wajh Bank 3	25.24035	36.93472	2011	19.3	82	0.47	2.09	0.70
	8	Wajh Bank	Wajh Bank 4	25.15465	36.91172	2011	27.5	75	0.44	1.88	0.64
	9	Umm Lujj	Marker 7 - 1	24.45313	37.19970	2011	7.0	88	0.53	2.39	0.75
	10	Umm Lujj	Marker 7 - 2	24.44277	37.20667	2011	20.5	86	0.46	2.05	0.70
	11	Umm Lujj	Marker 7 - 3	24.43110	37.22140	2011	20.7	72	0.43	1.82	0.61
	12	Umm Lujj	Marker 7 - 4	24.727	37.151	2011	20.2	82	0.59	2.58	0.81
Central	13	Seven Sisters	Abu Galawa	23.86382	37.88830	2008	27.9	85	0.38	1.70	0.56
	14	Seven Sisters	No Name	23.83428	37.89798	2008	30.1	81	0.42	1.86	0.70
	15	Seven Sisters	Shi'b Shabarir	23.78768	37.93590	2008	33.1	83	0.31	1.37	0.56
	16	Seven Sisters	Shib Sufmami	23.75252	37.96917	2008	33.2	72	0.38	1.64	0.69
	17	Rabigh	Maria's Reef	22.85080	38.72097	2008	16.0	85	0.43	1.89	0.70
	18	Rabigh	Khamsa 2	22.79837	38.61450	2008	28.6	78	0.46	2.01	0.78
	19	Rabigh	Noura	22.74988	38.61977	2008	31.2	79	0.47	2.06	0.79
	20	Rabigh	Bayeda long	22.72068	38.79622	2008	17.8	86	0.42	1.87	0.67

	21	Thuwal	3 Stick Reef	22.45928	38.90508	2008	18.2	82	0.74	3.28	0.94
	22	Thuwal	Al Mutarbej	22.42913	38.94718	2008	13.5	98	0.70	3.19	0.93
	23	Thuwal	Al Mutarbej South	22.39037	38.91820	2008	16.4	87	0.65	2.91	0.88
	24	Thuwal	Shi'b Nazar	22.37217	38.89715	2008	18.7	90	0.59	2.67	0.84
	25	North Jeddah	Madafi	22.05675	38.76688	2008	17.7	85	0.55	2.45	0.79
	26	North Jeddah	South reef	21.93408	38.86485	2008	9.17	98	0.58	2.65	0.84
	27	North Jeddah	Coral gardens	21.86748	38.75643	2008	20.9	95	0.63	2.89	0.91
	28	North Jeddah	Abu Terr	21.86605	38.85972	2008	12.3	94	0.69	3.15	0.91
South	29	Al-Lith	Mar Mar	19.84335	39.93358	2009	47.4	101	0.48	2.23	0.75
	30	Al-Lith	Dohra Island	19.82893	39.89853	2009	51.1	73	0.41	1.76	0.69
	31	Al-Lith	Al-Jadir	19.78848	39.95683	2009	49.4	87	0.41	1.81	0.63
	32	Al-Lith	Long Reef	19.76643	39.89223	2009	56.2	78	0.37	1.60	0.61
	33	Al-Qunfidhah	AQ4	19.15483	40.30113	2009	71.3	71	0.51	2.16	0.75
	34	Al-Qunfidhah	AQ3	19.10642	40.31775	2009	73.8	89	0.59	2.65	0.81
	35	Al-Qunfidhah	Murabit 1	19.02432	40.31792	2009	77.6	79	0.57	2.49	0.84
	36	Al-Qunfidhah	Petit Murabit	19.00238	40.28493	2009	81.5	73	0.45	1.95	0.66
	37	Ablo	Ablo 4	18.70673	40.65362	2009	57.0	88	0.57	2.56	0.84
	38	Ablo	Ablo 1	18.67510	40.73922	2009	50.1	85	0.66	2.94	0.89
	39	Ablo	Ablo 3	18.66772	40.65928	2009	58.9	82	0.50	2.20	0.75
	40	Ablo	Ablo 2	18.66500	40.81282	2009	41.6	83	0.62	2.75	0.82

Table 2

Sub-regions Compared:	Species	% Contribution to Dissimilarity	% Cumulative Contribution	Sub-region 1 mean abundance	Sub-region 2 mean abundance
North and Central	*Pseudoanthias squamipinnis*	7.9	7.9	5.2	9.3
Average dissimilarity = 38.4%	*Chromis dimidiata*	7.5	15.3	16.2	16.5
ANOSIM:	*Pseudochromis fridmani*	4.8	20.1	5.7	6.1
Global R=0.212, p=0.009	*Chromis flavaxilla*	3.6	23.6	4.7	5.4
	Chromis viridis	2.9	26.5	2.1	2.5
North and South	*Chromis dimidiata*	5.1	5.1	16.2	17.9
Average dissimilarity = 39.2%	*Pseudoanthias squamipinnis*	4.9	10.0	5.2	6.6
ANOSIM:	*Chromis flavaxilla*	4.5	14.5	4.7	7.6
Global R=0.651, *p*=0.001	*Eviota guttata*	3.4	17.9	0.3	3.5
	Pseudochromis fridmani	2.8	20.7	5.7	5.8
	Chromis viridis	2.5	23.2	2.1	2.2
	Chrysiptera unimaculata	2.3	25.4	0.3	2.3
Central and South	*Chromis dimidiata*	7.0	7.0	16.5	17.9
Average dissimilarity = 42.96%	*Pseudoanthias squamipinnis*	7.0	14.0	9.3	6.6
ANOSIM:	*Pseudochromis fridmani*	4.0	18.0	6.1	5.8
Global R=0.260, *p*=0.001	*Chromis flavaxilla*	3.8	21.8	5.4	7.6
	Eviota guttata	2.6	24.3	0.8	3.5
	Chromis viridis	2.4	26.7	2.5	2.2

Table 3

Sub-regions Compared:	Species	% Contribution to Dissimilarity	% Cumulative Contribution	Sub-region 1 mean abundance	Sub-region 2 mean abundance
North and Central Average dissimilarity =35.9% **ANOSIM: Global R=0.702, p=0.001**	*Xeniidae*	5.2	5.2	2	3.3
	Coralline (encrusting flat)	4.9	10.1	2.5	3.7
	Rubble (turf on rubble)	4.5	14.7	1.3	0.2
	Millepora	4.4	19	2.1	0.9
	Coralline (turf algae on rock)	3.8	22.8	6.5	5.9
	Sand	3.6	26.4	1.1	2.1
North and South Average dissimilarity = 36.8% **ANOSIM: Global R=0.7, p=0.001**	Coralline (encrusting flat)	4.9	4.9	2.5	3.7
	Coralline (turf algae on rock)	4.1	9	6.5	6
	Rubble (turf on rubble)	3.8	12.8	1.3	0.2
	Sponges (encrusting flat)	3.7	16.5	1.9	2.6
	Millepora	3.5	20	2.1	1.1
	Porites (encrusting columnar)	3.5	23.5	1.1	0
	Acropora (digitate)	3.4	27	1.7	0.6
Central and South Average dissimilarity = 34.5% **ANOSIM: Global R=0.501, p=0.001**	Coralline (encrusting flat)	4.6	4.6	3.7	3.7
	Xeniidae	4.5	9.1	3.3	2.7
	Sinularia	3.9	13	1.7	0.7
	Sand	3.9	16.9	2.1	1.3
	Sponges (encrusting flat)	3.8	20.6	2.3	2.6
	Coralline (turf algae on rock)	3.6	24.3	5.9	6

Table 4

	Top 25 species	North	Central	South
1	*Acanthurus nigrofuscus*	x	x	x
2	*Acanthurus sohal*	x	x	x
3	*Amblyglyphidodon indicus*	x	x	x
4	*Centropyge multispinis*	x	x	x
5	*Chaetodon austriacus*	x	x	x
6	*Chromis dimidiata*	x	x	x
7	*Chromis flavaxilla*	x	x	x
8	*Cirripectes castaneus*	x	x	x
9	*Ctenochaetus striatus*	x	x	x
10	*Gobiodon rivulatus*	x	x	x
11	*Gomphosus caeruleus*	x	x	x
12	*Halichoeres hortulanus*	x	x	x
13	*Labroides dimidiatus*	x	x	x
14	*Pomacentrus sulfureus*	x	x	x
15	*Pseudoanthias squamipinnis*	x	x	x
16	*Pseudocheilinus hexataenia*	x	x	x
17	*Pseudochromis fridmani*	x	x	x
18	*Pygoplites diacanthus*	x	x	x
19	*Thalassoma rueppellii*	x	x	x
20	*Chaetodon paucifasciatus*	x		
21	*Pseudocheilinus evanidus*	x		
22	*Naso elegans*	x	x	
23	*Plectroglyphidodon lucozonus*	x	x	
24	*Zebrasoma desjardinii*	x	x	
25	*Chaetodon auriga*		x	
26	*Chromis viridis*		x	
27	*Heniochus intermedius*		x	
28	*Myripristis murdjan*	x		x
29	*Paracirrhites forsteri*	x		x
30	*Thalassoma lunare*		x	x
31	*Cephalopholis hemistiktos*			x
32	*Chrysiptera unimaculata*			x
33	*Eviota guttata*			x
34	*Plectroglyphidodon lacrymatus*			x
	% Cumulative contribution	**76%**	**72%**	**72%**